

northern species in section *Myxocarpa* with $n = 7$ and the southern species with $n = 5$.

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CUSHION-LIKE FRUTICOSE LICHENS AS *DUDLEYA* SEED TRAPS AND NURSERIES IN COASTAL COMMUNITIES.—Richard E. Riefner, Jr. and Peter A. Bowler, Museum of Systematic Biology and Department of Ecology and Evolutionary Biology, University of California, Irvine 92717.

The species-rich lichen communities of the coastal bluffs and cliffs in California and Baja California, Mexico, are able to survive because of the ability of lichens to readily absorb moisture from coastal fog. Similar situations are found in the diverse lichen floras of maritime zones in many other regions experiencing a Mediterranean climate (Nash et al., Madroño, 26:149–163, 1979). The often dense growth of fruticose lichens, particularly saxicolous *Niebla* species (Ramalinaceae), provides an interesting and unique micro-habitat. *Niebla ceruchooides* is a well known, easily recognized coastal saxicolous lichen occurring from northern Baja California, Mexico, to the San Francisco Bay region in northern California (Bowler et al., Phytologia 77:23–37, 1994). This species is identified readily by either its cushion-like fruticose thallus 1–2 cm high or a larger 3–4 cm high more open bush-like morphology. The cushion-like lichen mats resemble miniature wind-trimmed coastal sage scrub vascular plants, and the lichens are similarly sculpted to some extent by their exposure to wind and fog along the coastal rocks and cliffs. Both growth forms are gregarious and are characterized by dichotomously branched, terete laciniae that rarely exceed 1 mm in cross-section. *Niebla ceruchooides* is especially abundant in summer fog zones from Punta Banda to Morro Bay.

During an ongoing investigation of the relict endemic vegetation of summer fog zone habitats in the California Floristic Province by the senior author, observations of micro-habitats in which several *Dudleya* species occur indicate that an interesting association exists between a number of coastal, cliff-dwelling *Dudleya* taxa and *N. ceruchooides*. Apparently the dense, intricately branched thallus of this lichen effectively captures minute *Dudleya* seeds as they are dispersed in their seasonal seed rain across rock outcrops. The lichen cushion provides a foothold for the seedlings and possibly an enriched nutrient seed bed that encourages propagation of *Dudleya* seedlings on otherwise sheer rock. The resulting consolidation of soil allows additional humus accumulation and further plant colonization. The expanding *Dudleya* caudex fragments the lichen thallus and enhances dispersal of the lichen. This process is mutually beneficial by making additional lichen cushions available for colonization by *Dudleya*. Seed capture by the thallus may decrease the fortuitous dispersal of *Dudleya* seeds to unfavorable habitats, possibly contributing to the viability of several locally endemic *Dudleya* taxa. Other possible ways in which the micro-bushes of lichen could increase germination and recruitment success of *Dudleya* species include greatly increasing the presence of water available to the seedling due to fog capture (lichens are known to rapidly absorb moisture equal to 150%–1200% of their dry weight; Hawksworth and Hill, The Lichen-forming Fungi, 1984), and the protection of young plants from snail and slug herbivory. The cushions of lichen are particularly well suited for trapping soil particles that build a suitable substrate for vascular plant growth.

Large, reproductively viable populations of *D. stolonifera* in Orange County, *D. verityi* in Ventura County, *D. caespitosa* in San Luis Obispo County, and *D. anomala* and *D. campanulata* in Baja California Norte are consistently associated with exten-

sive populations of *N. ceruchoides*. *Niebla homalea*, a common saxicolous fruticose lichen, has broad flat or angular blades and a more open thallus, thus only occasionally acts as a seed trap. Seeds of annual grasses, such as *Muhlenbergia microsperma*, are also trapped and germinate in lichen cushions. Transplantation of the *Dudleya* seedling-lichen cushions may be useful in mitigation, restoration, and enhancement projects of coastal cliff and scrub habitats where other methods, such as rock-boring, have failed.

Fruticose lichen species of the saxicolous communities along the Pacific fog belt may enhance entrapment of intersystem nutrients such as atmospheric aerosols and occult precipitation that might otherwise escape deposition upon cliffs and outcrops in coastal ecosystems. The importance of the saxicolous lichen community, however, has been relatively unexplored in its role in mineral cycling and fog drip potential. Hypothetically, extensive mats of *Niebla* may influence the quantity and chemistry of precipitation throughfall in saxicolous habitats, thereby potentially affecting vascular plant abundance and diversity. Experiments are being designed by the authors to ascertain the importance of fruticose saxicolous lichen populations in nutrient cycling in the California Floristic Province.

The dense intricate branching of the fruticose *N. ceruchoides* in coastal communities may be especially effective in intercepting particulates, aerosols, and gleaning moisture and nutrients from fog. Munger et al. (*Journal of Geophysical Research* 88:5109–5121, 1983) report that fog water may contain greater concentrations of nutrients than precipitation. Specialized fog-entrapping morphological adaptations are best known in the pendulous *Ramalina menziesii*, which has net-like reticulate fenestrations that effectively harvest moisture and nutrients from fog.

Azevedo and Morgan (*Ecology* 55:1135–1141, 1974) have identified summer fog as an important factor affecting water balances and nutrient cycling that in turn may influence species composition in coastal ecosystems. The capability of lichens to assimilate nutrients from rainwater, fog, particulates, and aerosols is well documented (Pike, *Bryologist* 81:247–257, 1978; Reiners and Olson, *Oecologia* 63:320–330, 1984; Lindberg et al., *Science* 231:141–145, 1986; Boucher and Nash, *Botanical Gazette* 151:114–118, 1990). The additional nutrients captured by these processes become available upon death and decomposition of the lichen or leached by precipitation and deposited on the surrounding soil/rock crevices. Corticolous lichens play a major role in nutrient cycling of numerous forest ecosystems. Knops et al. (*Lichenologist* 23:309–321, 1991) concluded that epiphytic lichens influence the amount and the chemistry of throughfall, and are important at the ecosystem level in capturing nutrients; saxicolous lichens may also prove to be as important in Pacific coastal communities.

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